

PREDATION ON GRAPTOLOIDS: NEW EVIDENCE FROM THE SILURIAN OF WALES

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ABSTRACT. New evidence for predation on graptoloids is presented from collections made from the uppermost Llandovery and lower Wenlock of Wales. *Mediograptus morleyae* occurs in dense ovoid masses, interpreted as faecal pellets. Rhabdosomes of both *M. morleyae* and *M. cf. inconspicuus* occur folded, with a stipe length of a few thecae between folds: these specimens may have a faecal origin, or may represent rhabdosomes dropped during manipulation prior to ingestion. The predation appears to have been species specific: none of the other species present in the collections is affected. The identity of the predators is uncertain.

Fossil graptoloids represent the dominant preserved macrozooplankton of the Ordovician to Lower Devonian. When alive, they presumably constituted a large reserve of accessible energy within the water column, and hence a major utilizable source for pelagic or nectic predators' (Underwood 1993, p. 195). Surprisingly, however, very little evidence has been presented to suggest that graptoloids were preyed upon (see Underwood 1993 for review). By way of explanation, Bates and Kirk (1985, p. 213) have suggested that graptolite periderm may have been 'tough and unattractive to predators' and that the graptoloids' soft tissues may have been 'poisonous, perhaps with warning coloration'.

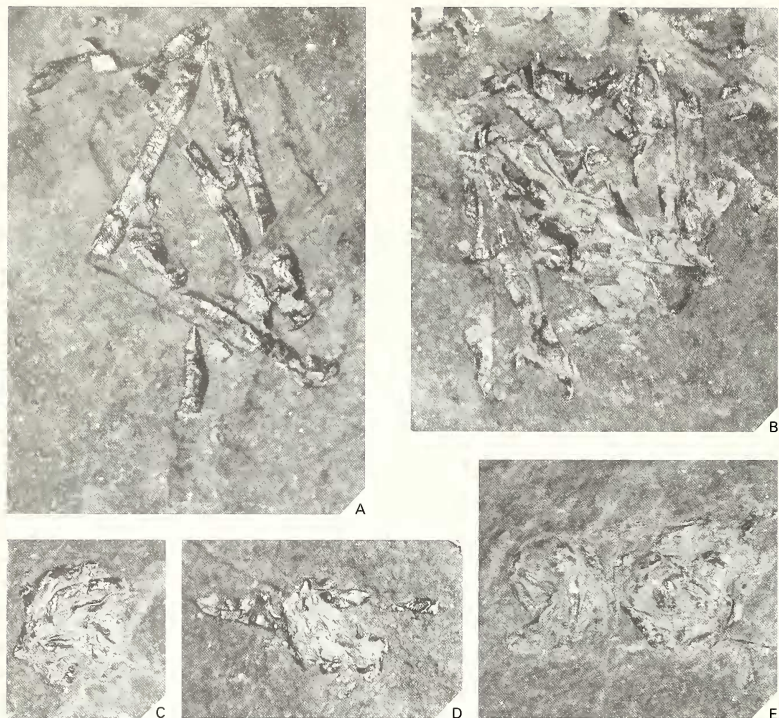
Evidence for predatorial attack on dendroid graptolites, however, appears not to be uncommon (Bull 1996), suggesting that graptolite periderm and/or soft tissue was not unpalatable to all predators. Dendroid graptolites were benthic and are characteristic of shallow marine environments, often with no graptoloid graptolites present (e.g. LoDuca 1995). It is probable therefore that organisms which fed upon dendroids would not have preyed also upon graptoloids which lived in an entirely different habitat (in the pelagic realm) and usually are found in deeper marine facies than are dendroids.

NEW EVIDENCE FOR PREDATION ON GRAPTOLOIDS

Description of new material

New evidence for predation on graptoloids is provided by specimens from two occurrences in Wales: the uppermost Llandovery (*insectus* Biozone) of the Banwy River section (Loydell and Cave 1996; material housed at the British Geological Survey, Keyworth, prefix BGS); and the lower Wenlock (*centrifugus* Biozone) of a quarry south-west of Disserseth (see Loydell and Cave 1993 for locality details; material collected by Jonathan H. Harris and housed at the Sedgwick Museum, Cambridge, prefix SM). All the material is well preserved, mostly as three-dimensional pyrite internal moulds with original periderm adhering.

The uppermost Llandovery specimens. *Mediograptus morleyae* Loydell and Cave, 1996 is the most abundant graptoloid in the highest graptoloid-bearing band within the Llandovery of the Banwy River section, comprising approximately 40 per cent. of the graptoloids collected (160 specimens out of a total of 363 graptoloids; the material was collected by bulk sampling, with no collector bias). Most rhabdosomes are undistorted. Fourteen specimens, however, occur as dense, ovoid masses; another 16 rhabdosomes are folded-up, with the straight rhabdosome sections between folds



TEXT-FIG. 1. *Mediograptus morleyae* Loydell and Cave, 1996; uppermost *insectus* Biozone graptoloid band (uppermost Telychian), Banwy River section, Wales; specimens showing evidence for predation. A–B, folded specimens; $\times 20$. A, BGS RCV7168. B, BGS RCV7201. C–E, dense ovoid masses, interpreted as faecal pellets; $\times 10$. C, BGS RCV7164. D, BGS RCV7193. E, BGS RCV7099 (two pellets).

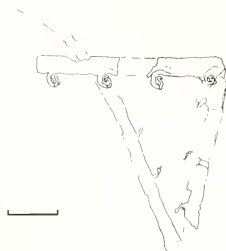
bearing two or three thecae. All these specimens can be identified confidently as *M. morleyae* by their very distinctive thecal morphology, still clearly visible on many specimens despite the distortion (e.g. Text-fig. 1A). The dense, ovoid masses (Text-fig. 1C–E) show less variation in dimensions (Table 1) than the folded specimens (Text-fig. 1A–B). Some of the latter have dimensions similar to those of the dense masses (e.g. BGS RCV7015, 3.5×2.4 mm); others, however, are significantly larger and elongated (e.g. BGS RCV7071, 7.0×1.7 mm).

The lower Wenlock specimens. Several folded specimens of *Mediograptus* cf. *inconspicuus* (Bouček, 1931) are present in the Harris collection. Their appearance (Text-fig. 2) is similar to that of the folded specimens from the Banwy River section, although the folds are fewer and more widely spaced. Dense, ovoid masses are not present in the collection.

TABLE 1. Maximum dimensions (in mm) of dense, ovoid masses (*Mediograptus morleyae*, uppermost Llandovery, Banwy River section). Accurate measurements of the other three specimens could not be made (because of damage, or the presence of other graptoloids superimposed).

| Specimen number | Length | Width |
|-----------------|--------|-------|
| BGS RCV7014 | 2.1 | 1.8 |
| BGS RCV7015 | 2.1 | 1.4 |
| BGS RCV7038 | 2.1 | 1.55 |
| BGS RCV7070 | 2.9 | 2.45 |
| BGS RCV7073 | 2.35 | 1.15 |
| BGS RCV7099(1) | 2.2 | 2.0 |
| BGS RCV7099(2) | 2.5 | 2.3 |
| BGS RCV7164(1) | 2.45 | 2.4 |
| BGS RCV7164(2) | 3.0 | 2.8 |
| BGS RCV7193 | 2.3 | 1.6 |
| BGS RCV7197 | 2.25 | 1.6 |

TEXT-FIG. 2. *Mediograptus* cf. *inconspicuus* (Bouček, 1931); SM X.272513; *centrifugus* Biozone (lower Wenlock), quarry south-west of Disserth, Wales; folded specimen. Scale bar represents 1 mm.



DISCUSSION

Interpretation of the material. The dense ovoid masses are, most probably, faecal pellets; their uniform, ovoid shape and similar dimensions support this conclusion. The simply folded specimens are more problematical. They too may represent coprolitic material, but alternatively perhaps represent specimens which had not passed through the gut, but were dropped during manipulation prior to ingestion. The folded graptoloid rhabdosomes would probably have reached the bottom rapidly (see Bates 1987 for discussion of graptoloid density).

Species selectivity. More than 200 specimens from eight other graptoloid species (of the genera *Retiolites*, *Monograptus*, *Monoclimacis* and *Cyrtograptus*) occur on the same bedding planes as do the predated *Mediograptus morleyae* specimens. None of these is folded or distorted in any way. Indeed in the entire Banwy River collection (more than 8000 graptoloids) only one other specimen (RCV3640; *Monoclimacis limmarssoni* (Tullberg, 1883), from the lowest part of the *insectus* Biozone) shows either of the features described above: in a total length of 24 mm, the rhabdosome exhibits two approximately right-angled kinks. Similarly, *Mediograptus* cf. *inconspicuus* is the only taxon within the lower Wenlock collection (many hundreds of graptoloids) to exhibit folded rhabdosomes.

It would seem that these two species of *Mediograptus* were being selected by predators in preference to other graptoloid taxa. Possibly, this was because of their rhabdosome tenuity, which allowed them to be folded up easily. *M. morleyae* has a maximum dorso-ventral width of only 0.4 mm. *M. inconspicuus* attains greater dorso-ventral widths (0.6–0.7 mm), but prothecal widths are

characteristically half the dorso-ventral width at the metatheca. Rhabdosome width can be only part of the explanation for the apparent selectivity, however, as there are many other graptoloids with narrow rhabdosomes or prothecae, none of which shows signs of predation. Perhaps only these *Mediograptus* species inhabited the same part of the water column as the predators; or possibly they lacked an adequate defence mechanism. Unfortunately, these hypotheses would be difficult, if not impossible, to test.

Possible predators. All the material described above occurs within laminated hemipelagites, deposited under low-energy conditions. Neither shelly benthic organisms nor trace fossils are present in the uppermost *insectus* Band in the Banwy River or in the graptolitic horizons in the quarry south-west of Disserth. Brachiopods and other shelly benthos do occur at other horizons within the Banwy River section (Temple 1987; Loydell and Cave 1996), and bioturbation is ubiquitous throughout much of the Upper Llandovery of this section; where this has penetrated graptolitic mudstones (e.g. those of the *spiralis* Biozone), the *Chondrites* mottling is obvious. We thus consider it unlikely that there was any macrobenthos alive at the time of deposition of the hemipelagite, although it is of course possible that any bedding parallel trace fossils have been obliterated by compaction during diagenesis, and thus we cannot discount completely that the features described above are the result of scavenging of the dead graptoloids by a benthic or nectobenthic soft-bodied organism.

Assuming that the graptoloids were preyed upon in the pelagic realm, what organisms could have been responsible? Graptolitic horizons in the Banwy River section have yielded a few simple coniform conodont elements. Conodonts are generally rare in graptolitic facies, and thus their occurrence here is interesting. However, the *Mediograptus* specimens show no evidence of any damage, other than the folding, which seems inconsistent with predation by a conodont animal (see e.g. Aldridge and Purnell 1996, p. 466).

Fossil nectic predators which are encountered regularly in the graptolitic facies of Wales are nautiloid cephalopods, represented almost exclusively by orthoconic forms. Feeding by extant cephalopods is generally destructive, involving crushing or breakage by powerful jaws prior to ingestion (Fretter and Graham 1976). Despite the remarkable abundance of cephalopod jaws in some Recent marine sediments (Clarke 1962), they are generally not common in the fossil record. Frey (1989) has suggested that the 'probable noncalcified nature of most Palaeozoic cephalopod mandibles does not indicate that Palaeozoic nautiloids were not carnivorous in habit, but that they fed primarily on soft-bodied organisms or organisms with weakly mineralized exoskeletons such as trilobites and other arthropods.' Frey (1989) attributed damage to Ordovician trilobites to predation by nautiloids, whilst Watkins (1991) interpreted ellipsoidal masses of broken skeletal fragments and crinoid ossicles as possible cephalopod 'cough-balls', ejected from the stomach via the mouth. As mentioned above, the *Mediograptus* specimens show no signs of having been bitten, or of other breakage.

Having suggested that appearance of the *Mediograptus* specimens described here is unlikely to be the result of predation by conodont animals or cephalopods, the implication is that predation was by a soft-bodied organism, which has left no trace in the rock record. It will be interesting to see whether the gut contents of any of the soft-bodied organisms from the recently discovered Silurian Konservat Lagerstätten in Wisconsin (Mikulic *et al.* 1985a, 1985b) and Herefordshire, England (Briggs *et al.* 1996) provide further evidence for the identity of predators on graptoloids.

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